Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE FERAX GROUP OF THE GENUS SAPROLEGNIA[1]

A. J. PIETERS

(WITH PLATE 170, CONTAINING 2 FIGURES)

Nees von Esenbeck ('23) first separated the then known forms of water molds into two genera, *Achlya* and *Saprolegnia,* but, until the time of de Bary's first paper ('52) in 1852, this distinction was not recognized by subsequent workers; de Bary revived the classification of the older author. Meanwhile all forms of water molds had been called *Saprolengia ferax* or *Achlya prolifera,* without any clear distinction being made between these genera. In 1850, Thuret ('50) described the swarm spores of a form that he called *S. ferax* Kütz., and he figured, for the first time, the oogonia. Later de Bary ('81) referred to this figure when he renamed *S. ferax, S. Thureti.*

In 1857 Pringsheim (57) contributed to the literature the description of *S. monoica* with excellent figures; other forms of *Saprolegnia,* those without antheridial branches, he considered as belonging to *S. ferax.* In 1873 he stated that further observation had convinced him that there was no true specific distinction between the forms with an antheridium on every oogonium and those in which the antheridia are almost or quite wanting. They differ, he says, "only in the relative number of antheridia." He therefore grouped all forms of *Saprolegnia* with round, pitted, many spored oogonia into the "*ferax*" group.

In 1881, there appeared a paper by de Bary ('81) in which he united *S. monoica, S. torulosa,* and *S. Thureti* (*S. ferax*) into a group which he called the *ferax* group. He had not yet distinguished *S. mixta.* In his description of *S. monoica,* de Bary followed Pringsheim, but added that in some cases the antheridial branches arise from hyphae remote from the oogonium, or, in other words, are not androgynous.

---

[1] Contribution from the Botanical Laboratory of the Univ. of Mich. No. 147.

Pringsheim had maintained that if one starts with a form having antheridia and continues the culture for some time, the number of antheridial branches gradually decreases in successive cultures until finally one may have forms without any antheridia. De Bary, however, showed that in his work each form, when secured in a pure culture, maintained its distinctive antheridial characters unchanged and suggested that impure cultures explained Pringsheim's results. Among the members of his "*ferax*" group de Bary distinguished *S. torulosa* by the arrangement of the oogonia in chains, *S. Thureti* (*S. ferax*) by the single large round oogonia, almost none of which have antheridia, and *S. monoica* by the constant presence of androgynous antheridia.

At this time, de Bary did not yet recognize *S. mixta,* nor did he include *S. hypogyna* Pringsheim in the *ferax* group, although this species had been described by Pringsheim in 1873 as a variety of *S. ferax.* In 1888, however, in de Bary's last paper ('88), published after his death, he included in the "*ferax*" group *S. Thureti, S. hypogyna, S. monoica, S. mixta, S. torulosa, S. dioica* (*S. diclina* of Humphrey), and *S. anisospora.* Pringsheim had previously included in the *ferax* group all those forms having smooth, round, pitted, many-spored oögonia, differing only in the number of oögonia accompanied by antheridia. De Bary seems to have departed from the historical conception of the "*ferax*" group and added to it such forms as *S. anisospora* with unpitted oögonium wall, eccentric oöspores and zoöspores of two sizes.

I prefer to follow Humphrey ('92) who limits the "*ferax*" group to *S. ferax, S. mixta,* and *S. monoica,* and these are undoubtedly the forms included under this term by Pringsheim, although he did not recognize *S. mixta* as being distinct from *S. ferax.*

If we turn to the original descriptions to ascertain the limits of the species, we find that in all cases the oögonia are described as round, smooth, and pitted and with a varying number of oöspores. De Bary, indeed, states that the oögonia of *S. Thureti* (*ferax*) are generaly larger than those of *monoica,* but as between *mixta* and *ferax* no distinction based on the oögonia is made. The specific difference, as de Bary plainly states, lies in the number of oögonia accompanied by antheridia, *S. mixta* having antheridia on about one half of the oögonia, *S. ferax* scarcely ever producing antheridia, while the male organs are found on every oögonium of *S. monoica*. De Bary also calls attention to the fact that the hyphae of *S. mixta* are flaccid and delicate in appearance, while those of the other two species are stiff and strong.

De Bary is very careful to make it clear that *S. ferax* is not wholly without antheridia (see '81, p. 92), and it is because this qualification on the part of de Bary has been sometimes overlooked that we find such statements as that by Kauffman ('08) that *S. ferax* "is said to have *no* antheridia." The formation of oögonia in the empty sporangium cases, thus forming the so-called "cylindrical" oögonia is also not given by de Bary as a character distinctive of *S. ferax*. There doubtless are forms in which this phenomenon occurs more often than in other forms, but the character is of no specific value. Humphrey says of *S. mixta*, "antheridia . . . , absent from a part of the oögonia, sometimes from a large part."

My attention was first called to the question of what is *S. mixta* or *S. ferax* by Kauffman's paper ('08) in which on page 368 he describes a form as *S. mixta*, though 75–90 per cent. of the oögonia were accompanied by antheridia, while on the following page he describes another form in which the male organs were found on only 1 or 2 per cent. of the oögonia. In experiments with the latter form, Kauffman was able to increase the number of antheridia to 25 per cent. of the oögonia but no more. A strict interpretation of the original description of *S. mixta* would exclude both of the forms with which Kauffman worked, as would also be the case with those the writer has collected and on which he found never less than 80 to 90 per cent. of antheridia. Kauffman considered that his form F. must be a form of *S. mixta* because he found antheridia, although he recognizes the difference between his two forms and notes that the hyphae of his form "H." are "rather slender" (p. 368).

Klebs ('99) found that when he grew *S. mixta* in a solution of haemoglobin, no antheridia were produced and this has also been the experience of the writer. On the other hand, Prof. W. C. Coker, of North Carolina, has stated in correspondence with the writer that in a strain of *S. ferax* which he cultivated, he was able to get from 1 to 95 per cent. of antheridial oögonia, depending on the medium used.

In 1911 I collected at Heidelberg, Germany, a species which I determined as *S. ferax* because I failed to find any antheridia on fly cultures. From time to time I secured antheridia when the fungus was grown in artificial media but not until 1913, having carried the culture to Ann Arbor, did I note antheridia on a fly culture. This led me to question the identification and to reexamine the original material on fly, this having been preserved in alcohol; not one antheridium was to be found.

During that winter I collected a number of cultures from the various dishes of algae kept in the botanical laboratories at the University of Michigan. Each form was isolated by making a single spore culture and a number of these could be referred only to *S. ferax* although in no case were antheridia entirely wanting. To test the matter of the production of antheridia, fly cultures were prepared and kept in a cool room, and the oögonia having antheridia were counted by examining the culture in the dish under a 16 mm. objective and a 12 × eyepiece. With this combination the antheridia can be plainly seen and the culture does not need to be disturbed. The number of oögonia counted and the number with antheridia are recorded in the following table.

CULTURE NO.	DATE	TEMPERATURE	NO. COUNTED	NO. WITH ANTHERIDIA
25	Nov. 19, 1913	Cool (12°–15° C.)	200	11
21F	" 20, "	"	200	19
21F	" " "	Room Temp. (22° + C.)	200	0
28	" 19, "	Cool	100	4
28	" " "	Room Temp.	Many, not counted	0
17	(*S. mixta*)	" "	" " "	90% at least
33	Nov. 20, 1913	Cool	100	1
34	" " "	"	125	3
35	" 23, "	"	100	14
35	" " "	"	100	11
35	" " "	"	100	13

A second culture and count gave the following results:

CULTURE No.	DATE	TEMPERATURE	NO. COUNTED	NO. WITH ANTHERIDIA
21F	Dec. 9, 1913	Room temp. (22° + C.)	Many	0
21F	" " "	Cool (12°–15° C.)	100	15
21F	" 24, "	Room temp.	80	1 (doubtful)
25	" " "	Cool	100	9
25	" " "	"	100	12
28	" 18, "	"	100	3
28	" 24, "	"	100	3
28	" " "	Room temp.	60	0
33	" 18, "	Cool	100	2
33	" " "	"	100	6
33	" 24, "	Room temp.	100	4
34	" 18, "	Cool	100	2
34	" 24, "	Room temp.	100	7
34	" " "	" "	100	1
35	" 11, "	Cool	100	2
35	" " "	"	100	5
35	" 13, "	Room temp.	100	19
35	" 18, "	Cool	100	7
35	" " "	"	100	7
35	" 24, "	Room temp.	100	5
37	" 18, "	Cool	100	1
37	" " "	"	100	9
37	" 23, "	Room temp.	300	0

The average number of oögonia accompanied by antheridia in cultures grown at a low temperature (about 12° to 15° C.) is shown in the following table:

Culture Number	Average Percentage of Oögonia With Antheridia
21F	8
25	8.8
28	4
33	4
34	2
35	8.4
37	5

In all the cultures cited above, the oögonia were substantially alike, of the same size and pitting, with slight fluctuating variations. The vegetative parts and the sporangia were also alike, but all of these cultures differed strikingly from number 17 which I collected in Germany and number 82, collected at Ann Arbor and which proved to belong to the same species as 17. These two forms had a flaccid delicate mycelium just as de Bary described for *S. mixta* and as Kauffman noted in his culture "H." The pits on the oögonia, though present, were less prominent than on the oögonia of *S. ferax,* and antheridia, usually of diclinous origin, were found on at least 90 per cent. of the oögonia. It is not impossible that single oögonia of *S. mixta* might be confused with those of *S. diclina* Humphrey, which has diclinous antheridia on round, poorly pitted oögonia, but the latter species, which I collected at Ann Arbor as number 38, has, as de Bary and Humphrey state, the oögonia mostly at the ends of long hyphae, rarely lateral and never racemose, while the lateral racemose arrangement is the rule in *S. mixta.*

While it is probable that mistaken identifications may occur in the study of poor material of several of these species, the case is worst as between *S. ferax* and *S. mixta.* If the almost complete absence of antheridia in the one case and their presence on one half of the oögonia in the other is decisive in these species, then neither of the two forms studied by Kauffman nor those discussed in this paper belong to *S. ferax* or to *S. mixta.* At the same time, there is no doubt that such forms as my numbers 17 and 82 are quite distinct from the others and that numbers 21F, 25, 28, 33, 34, 35, and 37 all belong to the same species. The number of oögonia provided with antheridia may vary in the same form depending on the medium in which it is grown. As already stated, Klebs found that in *S. mixta* the number varied from 0 to 90 per cent., Coker in correspondence, and Kauffman in the paper referred to have also recorded such a variation. In my study of the forms determined as belonging to *S. ferax,* I found that oögonia-bearing antheridia were much more common on the parts of the mycelium near the body of the fly than on the outer portions of the mycelium, and also that the antheridia were much more easily seen when the culture was young than after it had grown rather old. Under the influence of low temperature, there were generally more antheridia than when the culture was kept at room temperature, about 22 degrees Cent. *Saprolegnia monoica* is said to have antheridia of androgynous origin on every oögonium, but when I grew this in 0.05 per cent. haemoglobin solution, the number of antheridia present varied from 0 to 17 per cent. of the number of oögonia. When a mycelium that had previously been grown in pea extract, was transferred to 0.01 per cent. haemoglobin plus *M*/200 levulose, the oögonia were small, but each one was accompanied by an antheridium and the latter was either diclinous or androgynous. When such a mycelium was transferred to a solution in which the levulose was replaced by an equal concentration of dextrose, the oögonia produced were fewer, but very much larger and not more than 5 per cent. had antheridia. It is evident then that the number of antheridia present may vary with conditions, and that there may also be a natural variability independent of food conditions; the place of origin of the antheridia is also variable. Shall we then go back to Pringsheim's notion and consider these all forms of the same species? To one who has carried many pure cultures of these organisms through several years and who has observed how quite constant each form is under a certain set of conditions, this is out of the question; the forms are different. It is evident that these species make up a group of closely related forms representing tendencies to vary along different lines. Of these, *S. monoica* has the most complete sexuality with antheridia of prevailing androgynous origin; *S. mixta* has less complete sexuality, antheridia of prevailing diclinous origin and a more delicate mycelium; while *S. ferax* represents a complex of forms in which the loss of sexuality has gone much further that it has in the other species. The members of this last subgroup are probably very numerous. There is, of course, no doubt but that the form studied by de Bary was as he described it, almost free from antheridia. The form studied by Coker differed slightly from the ones I had, and Dr. Kauffman has verbally stated that the form he collected as *S. ferax* had many barrel shaped oögonia. Altogether, there seem to be almost as many forms as cultures studied, but all agree in the small number of oögonia found with antheridia. There is no intergradation between the forms with few antheridia and those clearly belonging to *S. mixta,* with one half or more of the oögonia accompanied by antheridia. Furthermore, so far as records go and so far as my own experience goes, the forms with a large number of antheridia have always had the "slender" mycelium first described by de Bary. Until further work throws additional light on this matter I am inclined to believe that all the forms with stiff, strong mycelium and a small number of antheridia on fly cultures at a temperature of 12 to 15 degrees C. must be called *S. ferax,* while those with weak mycelium and with antheridia on one half *or more* of the oögonia belong to *S. mixta* as described by de Bary.

This merely recognizes the fact that this species is a complex of forms of which de Bary happened to find one, and in this form the loss of sexuality had gone further than in most of the members of the complex.

UNIVERSITY OF MICHIGAN,
ANN ARBOR, MICH.

LITERATURE CITED

Nees von Esenbeck, C. G., '23. Zusatz to a paper by Carus, C. E., Beiträge zur Geschichte der unter Wasser an verwesenden Thierkörpen sich erzeugenden Schimmel—oder Algengattungen. Nova Acta Acad. C. L. C. N. C., Bd. XI, Th. II, 1823. (Taken from Humphrey, *q. v.*)

Bary, A. de, '52. Beitrag zur Kenntniss der Achlya prolifera. Bot. Zeit., Bd. X, p. 473, and T. VII, 1852.

——————, '81. Untersuchungen über Peronosporeen and Saprolegnieen Beitr. zur Morph. und Phys. der Pilze, IV, Reihe 1881.

——————, '88. Species der Saprolegnieen. Bot. Zeit., Bd. XLVI, pp. 613, 1888.

Thuret, G., '50. Recherches zur les Zoospores des Alguez et les Antheridies des Cryptogams. Ann. Sci. Nat. Bot., 3rd Ser., T. XIV, p. 214, 1850.

Pringsheim, N., '57. Beiträge zur Morphologie und Systmatic der Algen. II. De Saprolegnieen. Jarb. für wiss. Botanik, 3d I, 1857.

——————, '73. Weitere Nachträge zur Morphologie der Saprolegnieen. Jahrb. für wiss. Bot., Bd. IX, p. 191, 1873–74.

Humphrey, James E., '92. The Saprolegniaceae of the United States. Proceedings of the Amer. Phil. Soc. 1892.

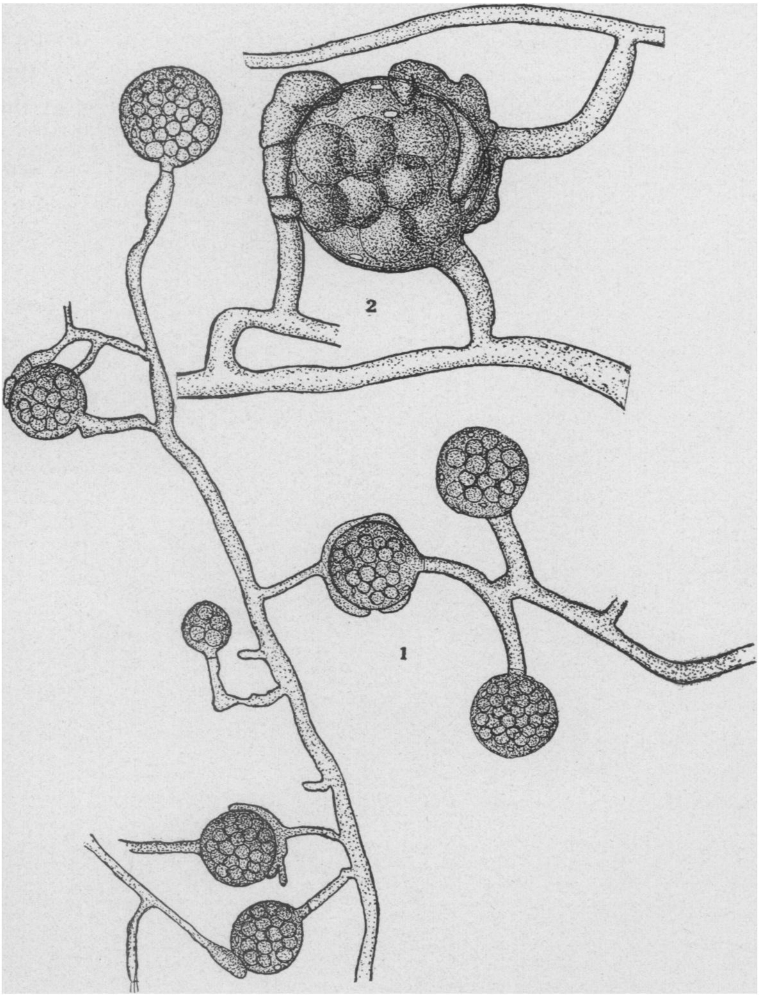
Klebs, G., '99. Zur Physiologie der Fortpflanzung eniger Pilze, II, Jahrb. für wiss. Botanik, 33, p. 513, 1899.

Kauffman, C. H., '08. A contribution of the Physiology of the Saprolegniaceae. Annals of Bot., Vol. XXII, July, 1908.

EXPLANATION OF PLATE CLXX

Fig. 1. *Saprolegnia ferax* (Gruith.) Thuret from fly culture in cool window of number 25; showing oögonia with androgynous and diclinous antheridia. × 167.

Fig. 2. Oögonium of *S. monoica* Pringsh. showing androgynous and diclinous antheridia on the same oögonium. × 440.



1. SAPROLEGNIA FERAX (GRUITH.) THURET
2. SAPROLEGNIA MONOICA PRINGSH.